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Journal

Proceedings. Biological sciences, 267(1444)

ISSN

0962-8452

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Publication Date

2000-04-01

DOI

10.1098/rspb.2000.1055

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The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish

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As a conspicuous evolutionary mechanism, sexual selection has received much attention from theorists and empiricists. Although the importance of the mating system to sexual selection has long been appreciated, the precise relationship remains obscure. In a classic experimental study based on parentage assessment using visible genetic markers, more than 50 years ago A. J. Bateman proposed that the cause of sexual selection in *Drosophila* is 'the stronger correlation, in males (relative to females), between number of mates and fertility (number of progeny)'. Half a century later, molecular genetic techniques for assigning parentage now permit mirror-image experimental tests of the 'Bateman gradient' using sex-role-reversed species. Here we show that, in the male-pregnant pipefish *Syngnathus typhle*, females exhibit a stronger positive association between number of mates and fertility than do males and that this relationship responds in the predicted fashion to changes in the adult sex ratio. These findings give empirical support to the idea that the relationship between mating success and number of progeny, as characterized by the Bateman gradient, is a central feature of the genetic mating system affecting the strength and direction of sexual selection.

Keywords: mating success; microsatellites; sexual selection; *Syngnathus typhle*; reproductive success

1. INTRODUCTION

In recent years, numerous papers have proposed various determinants of sexual selection including parental investment (Trivers 1972; Parker & Simmons 1996), the operational sex ratio (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996), variance in reproductive success (Payne 1979; Wade & Arnold 1980) and potential reproductive rates of the sexes (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992). However, most of these correlates of sexual selection have either been criticized as being poor measures of sexual selection (Sutherland 1985; Andersson 1994) or are impossible to quantify in a way which permits a meaningful comparative analysis (Andersson 1994; Andersson & Iwasa 1996). Furthermore, current theory lacks an established structure which connects these various features of a species' biology to the allocation of parentage within the sexes (i.e. the genetic mating system). Because a central feature of sexual selection is mating competition, a unifying framework is needed which relates the genetic mating system to sexual selection.

Bateman's (1948) perspective on the mating system of *Drosophila melanogaster* provided one empirical foundation for the development of mating system theory (Arnold & Duvall 1994). In *Drosophila*, the relationship between mating success and fertility differs substantially between the sexes (table 1). Mating success is defined here as the number of mates who bear or sire the progeny of a given individual and we adhere to Bateman's (1948) definition of fertility as the actual number of progeny produced by an individual during a well-defined breeding interval. In *Drosophila* males, the relationship between mating success and fertility appears linear, such that a male's reproductive success is limited primarily by the number of times he can mate. However, for females the relationship is much different, levelling off after a single mating. Thus, females are limited mainly by their intrinsic capacity to produce eggs and gain very little (in terms of offspring numbers) by mating with multiple males (but see Olsson *et al.* 1994; Trengenza & Wedell 1998). Bateman (1948) saw this difference between the sexes as the cause of sexual selection since it places a high premium on multiple mating by males and would promote selection favouring male competitive ability.

A recent theoretical integration of mating systems and formal selection theory pointed to the relationship between mating success and fertility as a cardinal feature in the process of sexual selection. A more detailed account is given by Arnold & Duvall (1994), but the key point for our purposes is that this important facet of the mating system is best characterized by the sexual selection gradient (also called the Bateman gradient) (Andersson & Iwasa 1996), which is given by the regression of fertility on mating success (figure 1). This gradient is a multiplicative component of the sexual selection which acts on traits. Thus, when the gradient is zero, there will typically be no sexual selection on any trait (but see Andersson 1994, pp. 157–158; Owens & Thompson 1994). However, when the gradient is steep some traits can experience strong sexual selection. Even though the relationship between mating success and fertility is apparently nonlinear for some groups (e.g. female *Drosophila*), the selection gradient is best estimated by a linear regression slope (Lande & Arnold 1983). In

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Received 27 October 1999 *Accepted* 13 December 1999
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Table 1. *Number of progeny produced as a function of mating success for* Drosophila (*from Bateman 1948*) *and* S. typhle *from our male-limited treatment* (*which includes the 6:2 and 4:4 female:male sex ratios*)

(Female *Drosophila* and male *S. typhle* do not gain from multiple mating in terms of progeny produced, whereas both male *Drosophila* and female *S. typhle* produce more progeny as a function of mating success. Only three female *S. typhle* had three mates, so the apparent decrease in fertility of these females is probably due to our limited sample size. Other evidence suggests that the positive relationship between mating success and fertility continues beyond two mates for female *S. typhle* (Berglund *et al.* 1989; Berglund & Rosenqvist 1990) (see figure 2). Sample sizes are in parentheses.)

	mean number of progeny produced by individuals				
species and sex	no mates	one mate	two mates	three mates	four mates
Drosophila males	0 (5)	45.2 (30)	77.0 (23)	125.0 (14)	—
Drosophila females	0 (1)	71.4 (28)	65.1 (39)	77.8 (4)	—
S. typhle males	0 (6)	52.3 (7)	45.4 (15)	54.9 (11)	54.7 (3)
S. typhle females	0 (26)	24.4 (19)	60.4 (14)	42.7 (3)	—

Drosophila, the male's Bateman gradient is steeper than the female's (figure 1).

Sex-role-reversed species, in which mating competition (and sexual selection) is stronger in females than in males, provide valuable opportunities for testing the generality of sexual selection theory (Williams 1975). One sex-role-reversed species which is amenable to experimentation is the pipefish *Syngnathus typhle*. As in its seahorse relatives, during copulation the *S. typhle* female transfers eggs to a pouch located on the ventral surface of the male where he fertilizes them and carries the resulting embryos until they are born several weeks later (Berglund *et al.* 1986*a*,*b*). Males thus have 100% paternity confidence (Jones & Avise 1997; Jones *et al.* 1999). Numerous laboratory experiments and field observations have shown that *S. typhle* is sex-role reversed: males tend to be choosy and females compete more intensely than males for access to mates (Berglund *et al.* 1986*a*,*b*; Berglund & Rosenqvist 1990, 1993; Vincent *et al.* 1994, 1995).

A priori, we should expect the sexual selection gradients of females to be steeper than those of males in a sex-role-reversed pipefish such as *S. typhle*. Thus, our main goal was to characterize the Bateman gradient in pipefish in an experimental framework similar to Bateman's (1948). Because the operational sex ratio is known to affect the sexual selection process, we also wanted to investigate the response of the sexual selection gradient to sex-ratio variation.

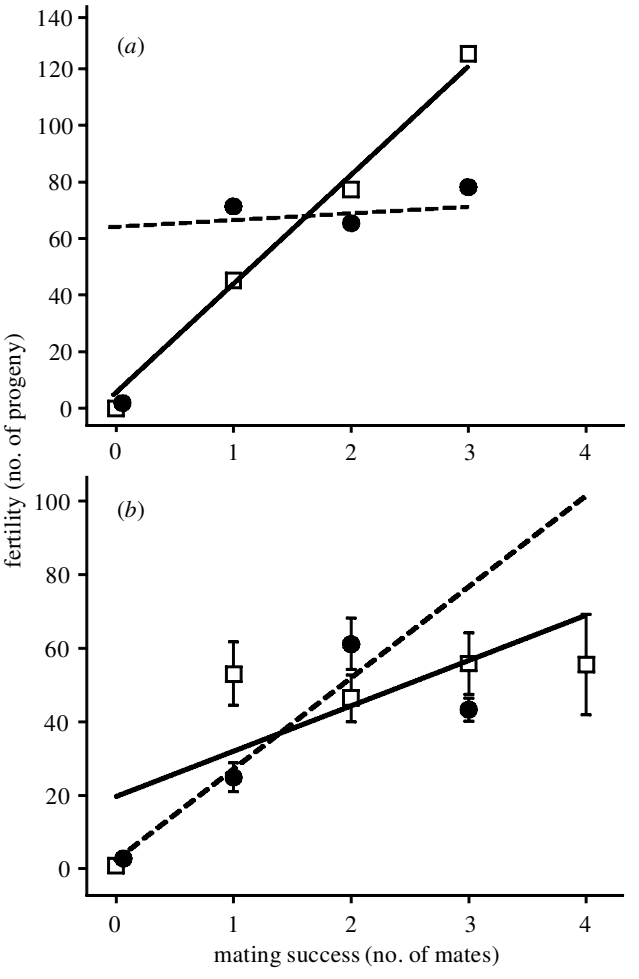

Figure 1. The relationship between mating success and fecundity. In both graphs, open squares represent males and closed circles represent females. Each symbol represents a mean (the sample sizes are given in table 1) and for *S. typhle* the error bars show one standard error. (*a*) Derived from Bateman's (1948) *Drosophila* data; for males $y = 3.1 + 39.5x$ and for females $y = 63.5 + 2.4x$. (*b*) Our results for male-limited *S. typhle* with $y = 1.4 + 24.1x$ for females and $y = 19.6 + 12.1x$ for males. The sexual selection gradient (Bateman gradient) is given by the weighted least-squares regression line relating mating success to fertility. The male Bateman gradients are shown as solid lines and the female gradients are shown as dashed lines. The non-zero slope in male *S. typhle* is almost entirely due to the six receptive males which failed to mate during the experiment. In *Drosophila*, the Bateman gradient for males is steeper than the gradient for females, indicating stronger sexual selection on males. However, in *S. typhle* the direction of sexual selection is reversed and the Bateman gradient for females is significantly steeper than the gradient for males ($F = 8.77$, d.f. = 1,100 and $p = 0.004$). The slopes for both the males and females are significantly greater than zero ($p = 0.001$ and $p < 0.001$, respectively).

2. METHODS

We collected unmated male and female *S. typhle* before the onset of the breeding season in May 1996 from the west coast of Sweden. Breeding experiments were conducted in 225 l barrels equipped with plastic eelgrass. Eight pipefish were placed in each barrel for a breeding period of *ca.* 72 h. The experiment included nine replicates of each of three different treatments: two males with six females, four males with four females and six males with two females. At the end of the breeding period pregnant males were removed from the barrels and placed in smaller holding tanks to allow embryonic development. The maternity of the embryos ($n = 2937$) was inferred by exclusion using two to four microsatellite loci. The precise assay conditions and primer sequences are reported elsewhere (Jones *et al.*

1999). Either every embryo or every third embryo in a male's pouch was analysed (a total of 1273 embryos). This sampling scheme recovers the parentage of all embryos with very little error because embryos are clumped by maternity within the pouch (Jones & Avise 1997; Jones *et al*. 1999).

3. RESULTS AND DISCUSSION

The results of the parentage analysis allowed us to examine the relationship between mating success and fertility in *S. typhle* (table 1). Our first two treatments (six females with two males and four females with four males) were statistically indistinguishable (comparison of male slopes $p = 0.41$ and comparison of female slopes $p = 0.45$). These treatments were therefore pooled as the 'male-limited' experiment for this analysis. Combining these treatments makes biological sense as well since laboratory experiments on the reproductive rates of the sexes indicate that, in a population of *S. typhle* with an equal or female-biased sex ratio, the ability of females to produce eggs far exceeds the available male brooding capacity (Berglund *et al.* 1989; Berglund & Rosenqvist 1990). Thus, in both treatments the sexual competition between females should have been intense. As might be expected for a species with sexual selection acting primarily on females, pipefish provide a striking contrast to *Drosophila* (table 1 and figure 1). Male *S. typhle* exhibit a relationship between mating success and fertility which closely resembles that of female *Drosophila* with no increase in fertility for males after the first mating. In contrast, the relationship for female *S. typhle* mirrors that of male *Drosophila* with a substantial benefit from multiple mating in terms of progeny production. In pipefish the female gender exhibits a significantly steeper Bateman gradient than the male (figure 1), a finding consistent with a reversal of the direction of sexual selection in *S. typhle*.

One salient feature of the Bateman gradient concept is that it provides for quantitative statistical evaluations of sexual selection between the sexes (as well as between populations or species) by a simple comparison of the slopes of regression lines. For example, our third treatment involved breeding trials with six males and two females per barrel. Pipefish males are known to respond behaviourally to variation in the operational sex ratio (Berglund 1994, 1995) and the two females in this treatment may not have produced enough eggs to impregnate all six males fully (Berglund *et al*. 1989; Berglund & Rosenqvist 1990). Under these circumstances we expect a reduction in the intensity of sexual selection on females and increased sexual selection on males (Vincent *et al*. 1994). Indeed, our results were consistent with these expectations. In this treatment, the Bateman gradients of the sexes did not differ significantly in slope, although the male gradient appeared to be slightly steeper than that of the female (figure 2). The fact that these gradients responded as expected to a change in the adult sex ratio lends additional support to the sexual selection gradient concept.

One important question in the implementation of the Bateman gradient is how to deal with individuals which fail to mate. Arnold & Duvall (1994) argued that individuals who are capable of mating but fail to obtain a mate should be included in the analysis, whereas individuals who are incapable of mating should be excluded. We tested males which failed to mate at the conclusion of the experiment by placing them in tanks with four females per male. If a male still did not mate, we considered him unreceptive and dropped him from the analysis. In the male-limited treatment, six males which did not mate during the experiment were found to be receptive and these males were included in the analysis (figure 1). If they had been excluded, the slope for the male gradient would have been very close to zero, indicating even less sexual selection on males (and still supporting our conclusions). In the male-excess treatment, enough males failed to mate that the inclusion or exclusion of non-receptive males did not change the results. The females were dissected at the end of the experiment to verify that they contained ripe eggs. All females appeared to be sexually receptive, so they were all included in the experiment. In fact, in the male-excess treatment all females mated ($n = 12$), suggesting that most if not all females used in this experiment were sexually responsive.

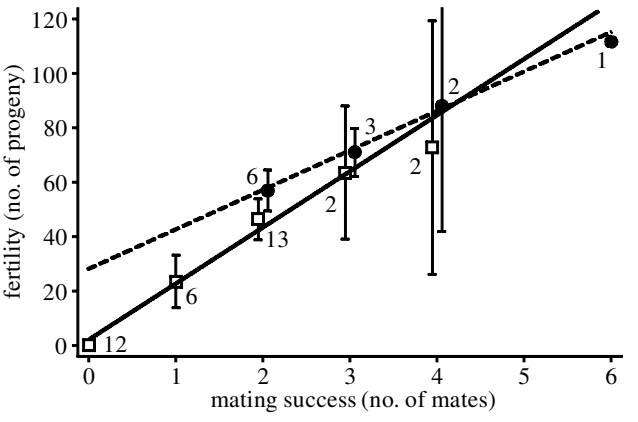

Figure 2. The Bateman gradients estimated for *S. typhle* in the male-excess treatment. Six males and two females comprised each mating group. The symbols and Bateman gradients are as described in figure 1. The numerals show the sample sizes associated with each mean. The male and female slopes are not significantly different from each other ($F = 0.77$, d.f. = 1,43 and $p = 0.39$), but are significantly positive (males $p < 0.001$ and females $p = 0.045$). For females $y = 27.7 + 14.5x$ and for males $y = 2.2 + 20.5x$.

Whereas *S. typhle* is clearly sex-role-reversed, one obvious difference between male *S. typhle* and female *Drosophila* is that male *S. typhle* display a non-zero sexual selection gradient. The positive slope for males in the male-limited treatment is due to a subset of receptive males which failed to mate and it indicates that weak sexual selection may be operating on male *S. typhle*. Consistent with this conclusion are the observations that female *S. typhle* prefer to mate with larger males (Berglund *et al*. 1986*b*) and that the unsuccessful males in our experiment were significantly smaller than the successful males (*t*-tests, male-limited treatment $p = 0.001$ and male-excess treatment $p = 0.004$).

4. CONCLUSIONS

Our results provide the first empirical test of the sexual selection gradient concept for a sex-role-reversed organism. Pipefish provide a clear contrast to *Drosophila*. In species with typical sex roles, we expect the Bateman

gradient of the males to have a steep slope relative to the gradient for females. As predicted, we found the opposite pattern for *S. typhle*. Females compete intensely for mates in this species (Berglund *et al*. 1989; Berglund & Rosenqvist 1993) and they also have a steeper sexual selection gradient. When an excess of males was present in the breeding population, a condition which should lessen the strength of sexual selection on females (Berglund 1994, 1995; Vincent *et al*. 1994), the difference between the gradients of the sexes disappeared. Thus, the sexual selection gradient accurately reflects sex-role reversal in *S. typhle* and responds as predicted to changes in the operational sex ratio.

Sex-role-reversed species provide critical tests of the generality of theories pertaining to the strength of sexual selection and the Bateman gradient concept has passed this first important test. The Bateman gradient surpasses some other important conceptualizations of the measurement of sexual selection in that, in principle, it can be quantified relatively easily through the use of molecular markers. In fact, for a large proportion of the dozens of biological systems to which modern parentage assessment techniques have been applied, the data for calculating sexual selection gradients may already exist. Thus, future work should focus on a broad comparative analysis of Bateman gradients among populations and species. Among other factors, parental investment, the operational sex ratio and potential reproductive rates are certainly important to the process of sexual selection, but perhaps they should be seen as affecting sexual selection through their impact on the realized relationship between mating success and fertility, Bateman's true cause of sexual selection.

We thank M. Sandvik, B. Nelson, Klubban Biological Station and Kristineberg Marine Station for assistance with this project. This work was supported financially by the National Science Foundation, the National Institutes of Health, a Pew fellowship, University of Georgia funds, a Norwegian Research Council grant and a Swedish National Science Research Council grant.

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